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Unveiling winter dormancy through empirical experiments☆

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ABSTRACT

Temperate woody perennials enter into a dormant status during winter in order to survive low temperatures. However, dormancy is not just a survival strategy, since cold winter temperatures are required for proper flowering. Global warming is having an impact on the phenology of woody perennials; warmer temperatures during dormancy may lead to an erratic reproductive behaviour due to the lack of chilling accumulated during winter. Although the relevance of dormancy for the adaptation of temperate woody perennials is well known, the biological processes behind dormancy remain unclear. In this work, we review how shoot and seedling experiments have contributed to the current knowledge on dormancy in woody perennials from the early discovery of the role of cold temperatures for adequate flowering to the latest knowledge on dormancy physiology and genetics. The information available has been organised in seven sections: (i) Climate change and winter dormancy in woody perennials; (ii) Discovering the importance of cold and the establishment of dormancy bases; (iii) Experiments to estimate the dormancy period; (iv) Exploring the physiology of dormancy; (v) Looking for biological markers for the dormancy status through histochemical techniques; (vi) Molecular biology of bud dormancy and (vii) Conclusions and perspectives.

1. Introduction: climate change and winter dormancy in woody perennials

One of the significant effects of global warming is the change in the phenology of woody perennials (Cleland et al., 2007). In temperate and boreal regions, rising temperatures during late winter and spring have caused earlier vegetative and reproductive timing, which continued into advance (Schwartz et al., 2006). However, warmer winters have unpredictable effects (Morin et al., 2010); mild temperatures during this period may lead to an erratic bud burst and blooming due to the lack of accumulated cold temperatures during winter dormancy. Temperate woody perennials enter a dormancy status during winter in order to survive low temperatures (Perry, 1971). However, dormancy is not just a survival strategy, since cold winter temperatures are required for proper flowering (Rohde and Bhalerao, 2007; Kurokura et al., 2013). Although the relevance of dormancy for the adaptation of temperate woody perennials is well known, the biological processes behind dormancy remain unclear (Considine and Considine, 2016).

Understanding dormancy is becoming a major issue for several scientific disciplines. From a biological point of view, the regulation of dormancy by temperatures could be involved in different processes, such as reproduction and flowering (Hedhly et al., 2009), photosynthesis (Gunderson et al., 2010; Tanino et al., 2014) and transport of nutrients (Schrader et al., 2004), since the timing of these processes needs to be adjusted to maximise the survival potential of the plant. Furthermore, changes in winter temperatures could affect the ecology from individual trees to whole ecosystems, since the timing of vegetative and reproductive phases is crucial to optimise seed set for individuals and populations (Hedhly et al., 2009). Changes in dormancy breaking may affect ecosystem stability since the cycle of some species may be altered. As a consequence, blooming periods may not be coincident, impeding adequate pollination and causing the emergence of new situations of competence for recourses (Cleland et al., 2007). Rising temperatures could extend the growing season in temperate and boreal forests (Menzel and Fabian, 1999) and disturb ecosystem-level carbon uptake (Stinziano and Way, 2017). In addition, fruit production is compromised by rising winter temperatures since the requirements of some cultivars are not being fulfilled (Campoy et al., 2011). In fruit tree species, the lack of a clear marker for the identification of breaking dormancy hampers the determination of chilling requirements of commercial cultivars, and hence the prediction of their adaptation to particular areas of cultivation, and the phenotyping of the progenies in those breeding programs whose objectives include the adaptation of cultivars to climate change conditions.

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Although dormancy can be approached from different points of view (biology, ecology and agriculture), a common methodology for the determination of the dormancy status is the use of shoots, seedlings, rooted shoots and young potted trees, which are usually used in experiments to observe whether buds recover their capacity to grow after a certain period of chilling. Dormancy has been studied in a wide number of tree species, depending on the purpose of each study. For agricultural studies, dormancy and chilling requirements are studied at the genotype level, due to the clonal propagation of the commercial cultivars (Atkinson et al., 2013). On the other hand, in forestry, dormancy is mainly studied at the population level (Way and Montgomery, 2015). Temperature conditions are highly variable among dormancy studies, since regions of interest include temperate and cold latitudes and climates, ranging from the mild winters of the Mediterranean regions (Gannouni et al., 2017) to the long freezing period of boreal areas (Man et al., 2016). This has led to a wide variety of experimental conditions, resulting in a large amount of information available concerning dormancy in woody perennials, which is highly dispersed and therefore impedes the integration of the results.

In recent years, different reviews on dormancy in woody perennials under a climate change context have been reported, focusing on agriculture (Atkinson et al., 2013; Campoy et al., 2011), forestry (Delpierre et al., 2016) and the molecular mechanisms involved in the process (Cooke et al., 2012). However, our understanding of dormancy is fragmented, and the biology behind dormancy remains elusive. In this work, we review how shoot and seedling experiments have contributed to current knowledge of dormancy in woody perennials from the early discovery of the role of cold temperatures for adequate flowering to the latest knowledge about dormancy physiology and genetics.

2. Discovering the importance of cold and the establishment of dormancy bases

Dormancy and the effects of chilling winter temperatures were discovered in the late 18th century to the early 19th century. Different experiments and approaches, in which potted plants or shoots of temperate woody perennials were exposed to warm temperatures during the winter period, showed unexpected behaviour of plants, attracting the attention of scientists and allowing the establishment of the early bases of dormancy.

The interest of T. Knight in the ascent of sap in woody plants in of the late 18th century led him to place potted trees of different temperate woody plant species commonly cultivated in England, such as apple (*Malus x domestica* Borkh.), pear (*Pyrus communis* L.) and vine (*Vitis vinifera* L.), under warm conditions. By monitoring changes in the phenology, he first established the theory that woody perennial plants had to abscise their leaves and be exposed to a certain period of cold for proper bud burst (Knight, 1801). Despite of the importance of these observations, it was not until more than a century later that dormancy studies acquired more importance. During the early 20th century, the fact that chilling was a prerequisite for flowering was more or less common knowledge, as revealed by Rosendahl (1914) in his attempt of obtaining flowers from herbaceous perennials during winter for his botanical classes at the University of Minnesota. His studies also showed the differences in chilling requirements between species and the role of dormancy in the adaptation of species to different latitudes (Rosendahl, 1914).

The first work specifically designed for the study of dormancy was performed in Washington by F. Coville (1920a), (1920b). After failure in obtaining two reproductive cycles per year in a blueberry (*Vaccinium corymbosum* L.) breeding program, he observed that warm temperatures during winter were unsuitable for bud burst and that the dormancy status was brought by cold temperatures. Based on this, Coville designed experiments with other species, such as grouseberry (*Viburnum americanum* Mill.), tamarack [*Larix laricina* (Du Roi) K. Koch] and crab [*Malus coronaria* (L.) Mill], by submitting seedlings, potted trees and shoots to different temperature conditions and by applying different treatments such as girdling, notching or rubbing, searching for substituting the effects of chilling. These experiments not only put in relevance the process of dormancy in temperate fruit production, allowed establishing that dormancy was a prerequisite for proper flowering and subsequent fruit setting (Coville, 1920a, 1920b). These experiments established a general method for further work.

After chilling fulfilment and dormancy breaking, a certain period under mild temperatures is required for growth resumption (heat requirements) (Perry, 1971). Modelling relating warm temperatures and phenological development was first established in the early 18th century (de Reaumur, 1735). Heat requirements were further incorporated to dormancy models for the prediction of bud burst (Richardson et al., 1974). The lack of a clear biological factor associated with the dormancy status has resulted in many terms and definitions of the process (Considine and Considine, 2016; Doorenbos, 1953; Lang et al., 1987; Samish, 1954; Vegis, 1964). Nowadays, the most used terms are those proposed by Lang et al. (1987): endodormancy, referred to when the regulation of dormancy is triggered by physiological factors; ecodormancy refers to dormancy regulated by environmental factors; paradormancy is used when growth inhibition arises from another part of the plant (e.g. apical dominance) (Lang et al., 1987). Recently, other terms have been proposed, taken in account other biological processes. Thus, Rohde and Bhalerao (2007) define dormancy as “the inability to initiate growth from meristems under favourable conditions”. Also, quiescence is referred to as a condition of repressed cell division, but growth would be resuming without delay under proper conditions. In this context, dormancy would represent a state of quiescence of meristematic or embryonic organs, in which growth is not resumed even under favourable conditions until after sufficient entrainment by environmental cues (Bewley, 1997; Considine and Considine, 2016).

The relevance of dormancy for forest and crop tree species has resulted in a number of experiments focused on the effect of temperatures on phenology and dormancy overcome.

3. Experiments to estimate the dormancy period

The general approach to determine when dormancy has overcome is based on evaluating phenology and bud growth in relation to time spent at low temperatures. Potted trees or shoots are transferred at different moments along winter to growth chambers with warmer temperatures. The date of breaking of endodormancy is established when bud growth is detected after several weeks under the respective growing conditions. This approach is time-consuming, and the delay in obtaining results is not suitable for many purposes, since the date of dormancy release is obtained several weeks after it occurs. Thus, this methodology has been combined with different mathematical models that quantify chilling temperatures along winter in order to determine the chilling requirements of particular genotypes for the prediction of dormancy release in other years.

Early experiments were performed using rooted shoots of pear (Bennett, 1949; Erez and Lavee, 1971) and later in peach (*Prunus persica* (L.) Batsch) (Couvillon et al., 1975) and blueberry (Mainland et al., 1977; Spiers, 1976), in which the breaking of dormancy was established when vegetative bud burst was observed after a period in the growth chamber. Bennett (1949) indicated that the requirements for dormancy release were a temperature between freezing and about 7.2 °C (45 °F), with a period of continuous exposure of two to three months. Other studies monitored flower buds rather than vegetative buds, most of them using peach shoots. In these experiments, the date of breaking of endodormancy was established when the flower buds, after several weeks in the growth chamber, increased significantly in weight (Brown and Kotob, 1957) or showed phenological development (Bennett, 1949).

To determine which temperatures are effective under field conditions, different models have been proposed to predict the response of buds of woody plants to chilling. Models for quantifying chilling accumulation are based on the effects of different temperatures on

dormancy completion. By this purpose, rooted shoots or small potted trees have been also used to evaluate different temperature conditions in growth chambers. Weinberger (1950) considered that temperatures below 0 °C had no effect in breaking dormancy and defined the term "chilling hour" (CH) as one hour at or below 7.2 °C. In a further report, the author related the delay in bud burst to high temperatures during winter, suggesting that the chilling effect of chilling hours was partially reversible (Weinberger, 1967). Afterwards, fluctuating temperatures were proposed to be more effective in satisfying the chilling requirements, and further experiments were focused on the effects of different temperature ranges on breaking dormancy. Erez and Lavee (1971) indicated that 6 °C contribute more to rest completion than any other tested temperature, while 10 °C was efficient in 50% and 21 °C nullified the effect of the low temperature. The "Utah model" proposed the use of the "chilling-unit" (CU) as 1 h at 7 °C, with temperatures between 0 and 16 °C having a positive effect on the breaking of dormancy, with a maximum promotion at 7 °C, but warmer temperatures (> 16 °C) have a negative effect (Richardson et al., 1974). Both "chilling hour" and the "Utah model" have been used successfully in cool temperate zones. However, in southern regions with Mediterranean or subtropical climate, these models are less useful since the effect of winter mild temperatures are undervalued (Dennis, 2003).

Different experiments have been performed to explore the effects of high and mild temperatures during winter on dormancy release (Couvillon and Erez, 1985; Erez et al., 1979; Erez and Couvillon, 1987). The "dynamic model" is based on the results of these experiments and defines one "chill portion" (CP) as exposure to 6 °C for 28 h. The dynamic model proposes that chill temperatures accumulate by a two-step process. In the first step, an intermediate product promoted by cold temperatures is accumulated, which can be reversed by warm temperatures. Once a sufficient amount of the intermediate product has accumulated, chill portions are permanently fixed and cannot be negated by high temperatures (Fishman et al., 1987). These models mainly differ in the importance given to the sequence of temperatures during chilling accumulation. The same temperature is considered to have the same effect in both "chilling hours" and the "Utah Model", but in the "dynamic model", the same temperature may have different effects on the accumulation of chilling, depending on when it occurs (Luedeling, 2012).

The models previously described are commonly applied for temperate fruit trees. They were developed in peach and served to quantify the chilling requirements of other peach cultivars (Bruckner et al., 2010; Gilreath and Buchanan, 1981; Wagner et al., 2006). However, they have been also applied in other temperate fruits such as apple (El-Agamy et al., 2001; Ghariani and Stebbins, 1994; Mankotia et al., 2004; Severino et al., 2010), apricot (*Prunus armeniaca* L.) (Gao et al., 2012; Ruiz et al., 2007; Tabuenca, 1968), blackcurrant (*Ribes nigrum* L.) (Jones et al., 2015), grape (Londo and Johnson, 2014; Wang et al., 2014), pear (Arzani and Mousavi, 2008; Kretzschmar et al., 2011), plum (*Prunus salicina* Lindl.) (Tabuenca, 1967) or sweet cherry (*Prunus avium* L.) (Alburquerque et al., 2008; Cortés and Gratacós, 2008; Fadón et al., 2017; Tabuenca, 1983). These models are the most widely used ones for fruit trees, although there are many others (Bidabé, 1965; Cesaraccio et al., 2004; Legave et al., 2008). Some of them have been developed for particular species such as apple (Landsberg, 1974; Shaltout and Unrath, 1983), blackcurrant (*Ribes nigrum* L.) (Rose and Cameron, 2009) or blueberry (Mainland et al., 1977; Spiers, 1976).

Other models have been developed for forest species (Cesaraccio et al., 2004), such as *Picea sitchensis* (Bong.) Carr. (Cannell and Smith, 1986), red osier dogwood (*Cornus sericea* L.) (Kobayashi et al., 1982) and beech (*Fagus sylvatica* L.) (Kramer, 1994). In coniferous species, fluctuating temperatures are less effective in dormancy release than constant temperatures (Lavender and Cleary, 1974). In forestry, temperature modelling has been mainly focused on the prediction of the impact of global warming to the forest masses in temperate and boreal areas (Schwartz et al., 2006). In contrast with those models developed for fruit crops, the predictions are currently based on the phenology of the forest from a large year series in order to obtain future projections (Cleland et al., 2007).

A drawback of these models is that they do not fit equally well in different climates and latitudes (Dennis, 2003). They are usually selected according to the study region, although each species may present a different response to the same conditions (Heide, 2008). Until further knowledge of dormancy processes is reached, there is no agreement on when to begin and end recording temperatures (Dennis, 2003). Another shortcoming of these models is related to the fact that the biological mechanisms behind cold requirements remain poorly understood (Fadón et al., 2017b), and the use of young potted trees or shoots cannot entirely reflect the behaviour of adult trees in field conditions (Rodrigo and Herrero, 2002; Sedgley and Griffin, 1989). Although temperature models are widely used for the estimation of chilling requirements, other factors should be taken into account, such as plant physiology, region of study and season (Campoy et al., 2011). However, the use of these models, in spite of their constraints and their empiric nature, is adequate in temperate fruit crop management and selection of cultivars and has allowed deep insights into physiology of dormancy, which will be described in the following section.

4. Exploring the physiology of dormancy

Most studies focused on dormancy physiology in woody perennials followed a general methodological approach (Fig. 1). *Populus* has been established as a model tree for the basic biology of dormancy (Jansson and Douglas, 2007). Studies with agricultural purposes used temperate fruit trees, whereas spruces (*Picea* sp.) and pines (*Pinus* sp.) have been used in a number of forestry studies. Young potted trees, shoots and seedlings are usually first exposed to field conditions, although some studies use artificial conditions for dormancy induction. On one side, the dormant status is analysed on seedlings and shoots or single node explants periodically collected, which are exposed to warmer temperatures in growth chambers (Fig. 1a). Endodormancy is considered broken when flowers or vegetative buds show growth after a certain period of time in suitable conditions (see Section 2). Mathematical models are currently used to predict the duration of dormancy (see Section 3). On the other side, individual vegetative or flower buds are used to unveil physiological processes in relation to dormancy phases. The different approaches applied could be classified into three main groups: analytical techniques, histochemical observations under the microscope (see Section 5) and molecular biology methods (see Section 5) (Fig. 1b).

A first attempt in the understanding of dormancy was the study of phytohormonal changes. Phytohormones play an important role in plant growth and development, regulating seed and potato (*Solanum tuberosum* L.) vernalisation (Hemberg, 1949; Vanstraelen and Benková, 2012). A similar role of phytohormones was expected for buds of temperate woody perennials. A common approach in physiological studies has been the external appliance of different phytohormones (Li et al., 2003) or plant growth regulators (Bennet and Skoog, 1938; Doorenbos, 1953) to break dormancy and provoke bud burst. This has allowed the introduction of commercial products that are currently used in temperate fruit crop management, mainly at warm regions with insufficient winter chilling (Erez, 1995; Lloyd and Firth, 1993; Ruiz et al., 2010). This approach is hampered by the fact that external treatments have different effects depending on the dormancy status (Fadón et al., 2015a). The way of action of these products seems to be related with the action of phytohormones (Zheng et al., 2015), but the biological mechanisms behind these processes remain unknown, despite their effectiveness.

Another approach to study the role of phytohormones in relation to dormancy is the quantification of different compounds in the bud by analytical techniques (Barros and Neill, 1989; Li et al., 2004; Olsen et al., 1995). Alterations in abscisic acid (ABA) concentration have been

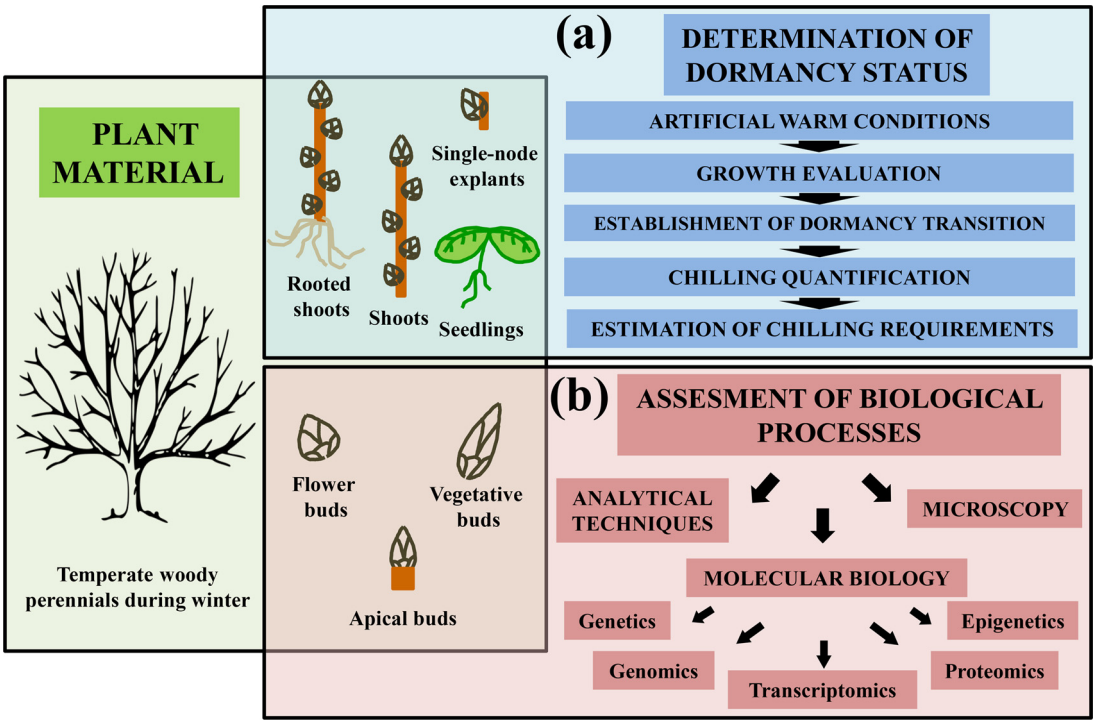

Fig. 1. Scheme of the experimental designs used to assess dormancy in temperate woody perennials. (a) Type of plant material used and steps for the evaluation of dormancy and the estimation of chilling requirements. (b) Type of buds used and approaches used for the assessment of the biological processes involved in dormancy.

related to leaf drop (Rinne et al., 2011; Welling et al., 1997). Growth cessation in the autumn and the establishment of dormancy has been associated with low levels of gibberellins (Eriksson and Moritz, 2002; Olsen et al., 1995). Although hormone regulation in relation to dormancy is still not well understood, the role of phytohormones in the regulation of same components of the cell cycle could influence the induction and breaking of dormancy (Horvath et al., 2003).

The analytical techniques have been also applied to the quantification of carbohydrates during winter dormancy (Bonhomme et al., 2005; Christiaens et al., 2014; Ito et al., 2013, 2012). Sugars such as glucose, fructose, sorbitol or starch have been analysed both in buds and in cambial tissues. The functional interest of carbohydrates in winter buds lies in their role in cold hardiness by regulating the osmotic balance (Flinn and Ashworth, 1995). The main drawback of analytical techniques is that a significant amount of sample is needed, and the small size of the buds and the heterogeneity of the different structures make it difficult to distinguish the activities of the different tissues. Histochemical techniques offer the opportunity to detect the activities of the different structures and tissues inside the buds thorough microscopic observations.

5. Looking for biological markers of the dormancy status through histochemical techniques

Different phases of bud dormancy occur under the same phenological stage of development, in which flower and vegetative buds are closed and covered by dark brown scales [stage A (Fleckinger, 1948) or 50/00 BBCH code (Fadón et al., 2015a; Meier, 2001)]. Thus, it is difficult to establish what is occurring inside the flower primordia during dormancy, since no external signs of development can be detected with the naked eye in either of these phases until budburst, when, depending on the species, the bud scales separate and the bud swells (Julian et al., 2010). To detect structural changes at different levels (organs, tissues, cells or cellular organelles), different studies have been performed by the microscopic observation of flower bud sections, using histochemical techniques.

Observations under stereoscopic microscopes have allowed to follow the meristem development of both vegetative (Sutinen et al., 2009) and reproductive buds in a dormancy context (Fadón et al., 2017, Saito et al.,2015). The vegetative buds of Norway spruce [(*Picea abies* (L.) Karst.] show the primordial needles tightly compressed against the primordial shoot, the tips show a rounded appearance, and the shaped apex is naked at the top of the bud (Sutinen et al., 2009). In sweet cherry, a flower developmental stage is conserved along dormancy, characterised by the presence of all the floral whorls clearly differentiated. The time the flowers remain at this stage differs between cultivars and is related to the chilling requirements and date of flowering (Fadón et al., 2017). Flower development is a consistent process in angiosperms, characterised in detail in model species (Smyth et al., 1990); recent studies have proposed a consistent flower development scale for the study of dormancy in *Prunus* (Fadón, 2015). The flower primordia developmental context could provide a solid base to frame the dormancy studies (Herrero et al., 2017).

Observations under light and fluorescence microscopes, combined with histochemical techniques, have been used in the search of biological markers associated with the dormancy status. Pollen development has been followed in different *Prunus* species to identify the mile stones of this process along the seasons. This has allowed showing that the sporogenous tissue is conserved in the anthers during dormancy (Fadón, 2015; Felker et al., 1983; Julian et al., 2011), and the timing of pollen meiosis seems closely related with the winter temperatures during dormancy (Citadin et al., 2002; Julian et al., 2014; Mirgorodskaya et al., 2015). The development of the pistil occurs later than that of the anthers. During dormancy, the different parts of the pistil are distinguishable: an incipient ovary, the style and the stigma still without papillae (Fadón et al., 2017). Inside the ovary, the ovules are not visible since they are developed later during the spring (Fadón, 2015).

Higher water availability makes tissues more sensitive to freezing temperatures (Ashworth and Wisniewski, 1991). This had led to study the role of water availability in dormancy. The characterisation of vascular tissue development of buds has showed that vessels remain

undifferentiated during the winter period (Ashworth, 1984; Begum et al., 2008, 2007; Julian et al., 2011). This has been also reported by the combined use of a magnetic resonance imaging system and microscopic observation (Saito et al., 2015).

Attention has been also focused on the cellular organelles and plastids during dormancy through the use of higher magnification. Differences in amyloplasts have been reported in different tissues, such as the connective tissue of the anther primordia (Fadón, 2015; Julian et al., 2011), the pistil primordia (Fadón et al., 2017; Felker et al., 1983) or the parenchymatous cells of the cortex (Rinne et al., 1994). The use of image analysis systems attached to the microscope allowed a relative quantification of carbohydrates at the tissue level (Rodrigo et al., 1997, 2000; Alcaraz et al., 2010, 2013); such an approach has been applied in dormancy studies. Thus, important variation in the starch content of the ovary primordia cells has been recently reported in sweet cherry flower buds. Starch accumulation follows the same pattern as chilling accumulation during dormancy, reaching a maximum at chilling fulfilment (Fadón, 2015; Herrero et al., 2017).

The use of electronic microscopy, combined with inmunolabeling, has allowed relating the cell-to-cell communication with dormancy regulation (Rinne et al., 2001, 2011). In apical buds of *Populus* and birch (*Betula pubescens* Roth), cells of the shoot apical meristems are individually isolated by plasmodesmata callose plugging. The subsequent exposure to chilling causes callose degradation and the restoration of the cell-to-cell communication (Rinne et al., 2001). Since the isolation of the cell through callose plugging of the plasmodesmata is a common mechanism of defence against different external agents (cold, wounds, insect injuries), further work was performed using seedlings under dormancy conditions. The characterisation of this process linked to dormancy has allowed the description of its genetics regulation (Rinne et al., 2011) and the accomplishment of a model of the perennial dormancy cycle in hybrid poplar (*Populus sieboldii* x *P. grandidentata*) (Paul et al., 2014). In the following section, we will describe the experiments that directly linked the dormancy status, determined by shoots or seedling experiments, with different molecular biology techniques to unveil the genetic regulation of dormancy.

6. Molecular biology of bud dormancy

Chilling requirements refer to the duration and depth of the cold required during dormancy, and they are specific for each cultivar, suggesting that they are under tight genetic control (Jansson and Douglas, 2007). To identify the causative genes for dormancy regulation, different experiments with shoots and seedlings, combined with molecular approaches, have been used (Shim et al., 2014), including genomics, genetics, transcriptomics, proteomics and epigenetics.

6.1. Genomics

Many genomic studies of dormancy are based on offspring seedlings from crosses between dormant and less-dormant parents. Dormancy phenotyping is usually characterised by the use of shoot cuttings and related to the chilling accumulated (see Section 3). To bridge the gap between phenotype behaviour and the genes behind, Quantitative Trait Loci (QTL) analysis has been developed in the progenies previously named. One of these progenies was obtained using as a parental an evergreen non-dormant mutant of peach, which shows continuous growth even under dormancy conditions (Rodriguez-A et al., 1994). Mapping of this character led to the proposal of the *DORMACY ASSOCIATED MADS-BOX* (*DAM)* genes as candidates for controlling the dormancy trait (Bielenberg et al., 2004; Bielenberg et al., 2008; Jiménez et al., 2010a). Other progenies have been obtained from divergent parents in *Prunus* species such as apricot (Fan et al., 2010; Gulick et al., 2009), almond (*Prunus dulcis* Mill.) (Sánchez-Pérez et al., 2012), sweet cherry (Castède et al., 2014) and peach (Romeu et al., 2014; Zhebentyayeva et al., 2014). One of the main aims of QTL analysis is not only the identification of target genes for subsequent genomic studies, but also the localisation of molecular makers to be used in plant breeding, since the offspring selection by phenotypical behaviour in relation to dormancy is difficult and time-consuming. On this point, the co-localisation of numerous QTLS with high effects with a small confidence interval in the Linkage Group 4 of sweet cherry may be useful to predict the adaptability to climatic conditions (Castède et al., 2015).

6.2. Genetics

To explore de role of target genes on dormancy, genetic studies are usually based on the use of seedlings of transformed *Populus* under different controlled conditions to phenotype the dormancy behaviour and monitor the bud burst dates. Thus, the role of the *DAM6* gene in dormancy has been confirmed, showing that its overexpression induces growth inhibitory functions (Sasaki et al., 2011). Target genes have been also selected between those involved in flower differentiation and flowering in *Arabidopsis thaliana.* Transformed *Populus* seedlings with the orthologues of *CONSTANS (CO)* and *FLOWERING LOCUS T (FT)* genes, which induced flowering in response to long days in *Arabidopsis* (Koornneef et al., 1991), have revealed that perennial trees regulate bud set and vegetative growth in response to the photoperiod (Böhlenius et al., 2006). Subsequent studies considered two similar poplar paralogs, *PtFT1* and *PtFT2*, to regulate these different functions (Hsu et al., 2011; Pin and Nilsson, 2012). The use of transformed olive with *FT* gene in relation to dormancy has also been recently studied (Haberman et al., 2017). The *CENTRORADIALIS1* (*CEN1)* gene has been selected in *Populus*, since it belongs to the same gene family of *TERMINAL FLOWER 1* (*TFL1*), which, in *Arabidopsis*, is expressed during the vegetative phase, delaying the commitment to form and inflorescence (Bradley, 1997; Jaeger et al., 2013). In *Populus*, the downregulation of *PopCEN1* enables dormancy release, and once growth is resumed, upregulation promotes meristem indetermination (Mohamed et al., 2010). The identification of those target genes, *DAM*, *FT*, *CEN*, has allowed the study of their transcription during the onset and release of dormancy transitions.

6.3. Transcriptomics

Analyses of transcriptome changes during the onset and release of dormancy transitions have allowed focusing the attention on the expression of the target genes previously associated with dormancy and on grouping the gene transcripts according their function at different dormancy phases. To unveil the role of the different *DAM* genes previously identified, their expression has been studied in relation to the environmental signals that regulate dormancy. A series of experiments using rooted shoots, under controlled conditions of photoperiod and cold temperatures, have shown that *DAM1*, *DAM2* and *DAM4* are related with seasonal cessation of elongation and terminal flower bud formation in late summer, and that *DAM3*, *DAM5* and *DAM6* function in establishing and maintaining endodormancy (Li et al., 2009). Genes *DAM5* and *DAM6* are up-regulated with short-day photoperiods, reaching a peak with chilling fulfilment and being subsequently down-regulated with bud break and blooming (Jiménez et al., 2010b). The expression of the *DAM* genes in relation to dormancy has also been studied in pear (Ubi et al., 2010) and sweet cherry (Castède et al., 2014). The role of *FT* and *CEN1* in the regulation of dormancy has been subsequently analysed by transcriptome analysis after the obtaining of the transformed trees, to ensure successful transformation and the expression of the genes (Mohamed et al., 2010; Hsu et al., 2011; Pin and Nilsson, 2012).

The comparative transcriptome analysis of pear genotypes with different chilling requirements has resulted in the selection of the same target genes involved in endodormancy maintenance and the transition from endo- to eco-dormancy, such as *Inducer of C-repeat binding factor*

expression 1 (*ICE1*), *ETHYLENE RESPONSE FACTOR* (*ERF*) and *dehydration-responsive element binding protein* (*DREB*) (Takemura et al., 2015).

The wide information obtained by transcriptomic techniques could be interpreted by analysis profiling, by grouping the gen transcripts according to their function at different dormancy phases. This approach has been used in several temperate woody perennial species such as apple (Porto et al., 2015), chestnut (*Castanea sativa* Mill.) (Santamaría et al., 2011), grape (Khalil-Ur-Rehman et al., 2017), hybrid aspen (Karlberg et al., 2010), peach (Leida et al., 2012), Japanese pear (*Pyrus pyrifolia* Nakai) (Bai et al., 2013; Liu et al., 2012; Saito et al., 2013) or raspberry (*Rubus idaeus* L.) (Mazzitelli et al., 2007). Differential expression along dormancy has been shown by genes related with stress responses (Karlberg et al., 2010; Mazzitelli et al., 2007; Santamaría et al., 2011), phytohormones (Karlberg et al., 2010; Khalil-Ur-Rehman et al., 2017; Mazzitelli et al., 2007), cell cycle and chromatin remodelling (Karlberg et al., 2010; Santamaría et al., 2011) or sugar transport and reserves (Horvath et al., 2008; Liu et al., 2015; Mazzitelli et al., 2007).

6.4. Proteomics

Proteomic analyses have identified proteins that appear to be involved in dormancy transitions. Proteomic profiles during winter have been obtained in different species such as blueberry (Arora et al., 1997), Japanese apricot (*Prunus mume* Sieb. et Zucc.) (Yamane et al., 2006; Zhuang et al., 2013) or white spruce [*Picea glauca* (Moench.) Voss] (Gonzalez et al., 2012). These studies have reported a consistently high expression of dehydrines during dormancy, which provide stability of the macromolecules under environmental stress. The expression of dehydrines has been related to dormancy regulation (Arora et al., 2003; Yamane et al., 2006) and cold acclimation (Kontunen-Soppela and Laine, 2001; Rowland et al., 2004; Yakovlev et al., 2008).

6.5. Epigenetics

There is growing evidence that epigenetic regulation is involved in dormancy in forest and fruit trees (Ríos et al., 2014; Shim et al., 2014). Different reports have showed similarities between the process of vernalisation in seeds and dormancy in buds (Ríos et al., 2014; Cooke et al., 2012). Both processes require a period of chilling for growth resumption, in which the regulation of *DAM*, *VERN* and *FT* genes has been associated with chilling requirements (Ríos et al., 2014). The expression of these genes in seeds of *Arabidopsis* has showed histone modification in relation to vernalisation (Yoo et al., 2005; Melzer et al., 2008). Epigenetic studies have been performed in different woody perennials such as the fruit trees peach (Badenes et al., 2012) and apple (Kumar et al., 2016) or in forest trees such as chestnut (Santamaría et al., 2011) and *Populus thrinocarpa* (Vining et al., 2012). These studies indicate that histone modification and DNA methylation might take place during various phases of the dormancy cycle and suggest that the same active growth-regulating genes might be repressed during dormancy induction through chromatin compaction, enhancing the dynamic nature of dormancy (Shim et al., 2014).

Molecular biology techniques, combined with shoot cuttings and seedling experiments, have significantly contributed to the knowledge about dormancy regulation. The high amount of information obtained is still fragmented, but it is an active field that will lead to a better understanding of the regulation of dormancy.

7. Conclusions and perspectives

Although the need of chilling accumulation for proper flowering has been noticed early (Knight, 1801; Coville, 1920a, 1920b), after two centuries of scientific interest in the dormancy of woody perennials, the interactions between the different biological processes occurring inside each bud are not completely understood (Shim et al., 2014). However, the increasing effort to understand dormancy has resulted in an enormous body of information, which has contributed to a better understanding of the dormancy process, but also shows the complexity of this phenomenon.

Dormancy regulation represents a significant physiological problem, which is critical for woody perennials and has important economic and environmental implications (Atkinson et al., 2013; Campoy et al., 2011; Luedeling, 2012). The rising concern about global warming and its effects on phenology in horticulture and forestry have renewed the interest in understanding flower bud dormancy (Cleland et al., 2007; Gilliam, 2016; Fadón, 2015). In this review, reports from 37 different species of woody perennials are presented, from Mediterranean and subtropical to boreal climates. Many different approaches of investigation have been used, showing that the information remains extremely fragmented in comparison with other biological processes, which are mainly studied in model plants under established conditions.

In fruit tree species, chilling requirements are important criteria in cultivar selection for a particular area (Atkinson et al., 2013). However, they are cumbersome to calculate, and the available data are highly variable depending on the conditions of the study region (Measham et al., 2017) and the model used (Seeley, 1994). This empirical knowledge has been widely used worldwide, but only in very few cultivars. The increasing number of new cultivars from fruit breeding programs emphasises the necessity of a proper biological marker. However, this is hampered by the lack of knowledge about the processes inside the flower bud and about the mechanisms and the changes underpinning dormancy. Improving our understanding about the reasons why chilling is required for proper bud development is crucial for understanding dormancy, but also for fruit production under a scenario of warmer winters with less chill accumulation.

Forests play an essential role in mitigating climate change impact by carbon uptake and retention (Bonan, 2008). Increasing temperatures and drought risks associated with climate change are expected to be the cause of migration and substitution of tree species (Bussotti et al., 2015). Current modelled simulation of future forest distribution suggests the expansion of forests to colder regions and the reduction in hotter and drier regions (Bussotti et al., 2015). However, natural migration of tree species may be hampered by several unpredictable factors like extreme weather events (Wieser et al., 2009), the changing roles of parasites and diseases, and the resilience of forests (Bumma and Wessman, 2013). Appropriate forest management is of fundamental importance to maintain ecologically stable forests in the future climatic conditions. Management strategies may include assisted migration through the selection of adapted provenances or the substitution of native with non-native species more suitable for the future climatic conditions (Bumma and Wessman, 2013; Bussotti et al., 2015), especially in those areas where forestry is of high economic value and significant climate changes effects are expected (Hanewinkel et al., 2013). Improving the understanding of the role of temperature and photoperiod in the regulation of dormancy, plant phenology and growth may be essential to evaluate future scenarios for assisted migration for the maintenance of the temperate forest areas (Way and Montgomery, 2015).

The need to understand the unpredictable effects of winter rising temperatures (Fu et al., 2015) has oriented efforts to understand the genetic regulation (Abbott et al., 2002; Shim et al., 2014) and the physiological mechanisms of bud dormancy (Paul et al., 2014; Herrero et al., 2017). However, the results are scattered and difficult to contextualise (Fadön et al., 2015b). Until now, the lack of accurate biological markers requires us to explore dormancy via shoot/seedling experiments. However, the low homogeneity among the different approaches reported and the techniques used make it difficult to frame the results in a biological context. This should be improved through a better knowledge of the internal development of the flower primordia and buds during dormancy while exposed to chilling temperatures

(Fadón et al., 2017, Saito et al.,2015). Likewise, efforts should be made to integrate the fragmented available information about dormancy by considering the whole annual cycle of trees as one continuous process, in which the conditions during bud formation, dormancy induction, bud dormancy and dormancy release have an effect on subsequent events after budburst (Viherä-Aarnio et al., 2014). Knowing the complex genetic and physiological processes involved in the dormancy of woody perennials, as well as their interactions, will have a great impact on fruit production and forestry by providing new tools for the adaptation of fruit trees and forests from temperate and cold zones to global warming conditions.

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